ANATOMY OF *ACMÆA TESTUDINALIS* MÜLLER

PART I. INTRODUCTORY MATERIAL—EXTERNAL ANATOMY

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Introduction

Some months ago I published in this journal under the title "Biology of *Acmæa testudinalis* Müller" an excerpt from a monograph of this species upon which I have long been engaged. I have now decided to publish the entire monograph in sections of which the present is the first. It should naturally be introduced by remarks upon the scope of the work but as these were prefixed to the earlier article, I refer the reader to that, adding merely that the investigation is intended not only as a contribution to a knowledge of the New England fauna but also as a first step in such a careful comparative study of the different species of the genus as is there suggested. This being its aim, it occupies itself in the main with anatomy, touching only incidentally upon either histology or embryology. I have, moreover, tried to make a paper which would serve as an introduction to the study of the neglected but fascinating group of Gastropoda. This aim will, I trust, serve as excuse for the admission of some material too elementary to be included in a paper addressed exclusively to specialists.

Zoölogical Position of Acmæa and its Allies

Acmæa belongs to the Scutibranchiata (Aspidobranchia, Diotocardia of Bouvier *et al.*), a suborder which includes all the more primitive Prosobranchiata and which is divisible into two sections: the Rhipidoglossa (Diotocardia of Remy Perrier) and the Docoglossa (Heterocardia). The only characteristics by which members of these two sections may infallibly be distinguished are first, the nature of the radula and second, the presence of dialy-

neury in the nervous system of the Rhipidoglossa and its absence in the Docoglossa. Dialyneury, it will be remembered, is the name applied to that form of nervous system in which the mantle is innervated in part from the pleural and in part from the visceral ganglia and in which these two systems of nerves are connected by anastomosis. It may be added that the ventricle in Rhipidoglossa is usually traversed by the rectum although the Helicinidæ, which have but one auricle, are an exception to this rule.

The Rhipidoglossa fall into two subsections: the Zygobranchia, characterized by the possession of two gills and two auricles, which are usually symmetrically disposed, although one gill may be smaller than the other; and the Azygobranchia with but one gill and ordinarily with two auricles, one of which is more or less rudimentary or even absent altogether. The Docoglossa have a single gill (ctenidium) or none at all, a single auricle with no trace of a second,[1] and a heart whose ventricle is never traversed by the rectum. It is thus evident that the three divisions of Scutibranchiata form in many respects a continuous anatomical series whose members, whatever the view as to their phylogenetic relationship, may often be profitably compared.

The Docoglossa[2] include three families: the Lepetidæ, Acmæidæ, and Patellidæ. The Lepetidæ is a small family whose members inhabit water of considerable depth. Of its fourteen species and varieties only one is recorded as living at low-water mark; the others have been dredged at depths varying from ten fathoms (five fathoms in one instance) to thirteen hundred ninety-five fathoms. While in certain respects, as in the shell and radula, they exhibit relationship to the Rhipidoglossa, in others they are modified in correlation with their environment so that they appear to be, as maintained by Dall, less typical Docoglossa than are the others. The family contains three genera: Lepeta, (including Pilidium), Propilidium, Lepetella.

The two remaining families are much larger and are typically

[1] Spillmann (:05, pp. 569–571) considers that he has found traces of a second auricle.

[2] In the classification of the Docoglossa I follow Pilsbry (Tryon and Pilsbry, '91).

litoral animals. The first one, the Acmæidæ, comprises those limpets which retain the primitive gill (ctenidium) with or without a cordon of branchial leaflets; the second, the Patellidæ, comprises those which lack a ctenidium but have a branchial cordon. The Acmæidæ contains three genera: Pectinodonta, with one species, a deep-sea form found off some of the West Indian islands; Acmæa, with eighty-four species, of almost world-wide distribution; Scurria (including the subgenus Lottia), whose five species are found only on the West American coasts, as far north as San Francisco. The Patellidæ contains also three genera: Patella (including the subgenus Helcion and the sections Patina, Scutellastra, Ancistromesus, all often regarded as genera), with forty-eight species which with one exception (*P. mexicana*) are entirely restricted to the Old World; Nacella, whose seven species are found only in the region about the southern part of South America; Helcioniscus, with forty-eight species in various portions of the Indian and Pacific Oceans but not extending on the American coast farther north than Chili.

History of Investigation

The name *Patella* (*Acmæa*) *testudinalis* first appears in 1776 in Müller's *Prodromus* but more than fifty years went by before any record was made of so obvious a feature in its anatomy as the possession of a ctenidium. It was the observation of this fact which led Eschscholtz to establish in 1830 the new genus Acmæa. As is well known, his early death left uncompleted the *Zoologischer Atlas* which was to have embodied the results accumulated during the years of his circumnavigating voyages. Such material as was in condition to be used by another was completed by his friend Rathke and published in 1833 as a fifth part of the *Atlas*. It contained an anatomical account, covering two folio pages, of the new genus Acmæa followed by brief descriptions, dealing with only the shells, of eleven species collected by Eschscholtz in the neighborhood of Sitka.

This first anatomical study is purely description and is of merely historic interest. The points touched upon are only the more

obvious ones; the account contains some unquestionable errors and some statements which if correct, do not apply to all members of the genus.

A step in advance was marked by Dall's successive papers on the limpets of which the first appeared in 1869. These papers deal mainly with the Acmæidæ and although preëminently systematic, contain occasionally anatomical facts of interest and importance.

The first considerable contributions to the morphology of Acmæa are contained, however, in two papers on the comparative anatomy of certain organs of Prosobranchs which issued from the laboratory of Professor E. Perrier about fifteen years ago. The first of these papers, (Bouvier, '87) dealt with the nervous system; the second, (Bernard, '90) with the pallial organs. Bouvier ('87, pp. 15–22) gives a full and careful description of the nervous system of Patella and in a single paragraph compares therewith the very similar one of *A. testudinalis.* Bernard describes in detail the osphradium and the innervation of the gill in a species of Tectura (Acmæa) and in the same connection figures and describes the arrangement of the principal ganglia in what he calls *T. fontainesi.* It should be noted that this latter species is without doubt, as I have shown elsewhere, (Willcox, :00) incorrectly named and that the identification of the other, so far as concerns the species, is questionable. The so called *Tectura fontainesi,* having circumpallial branchial lamellæ (Bernard, '90, p. 217) is of course not a true Tectura (Acmæa) but may very probably be a Scurria. *T. pileopsis,* Bernard's other species, is stated by him ('90, p. 217) to have come from Chili but that species is recorded by Pilsbry (Tryon and Pilsbry, '91, p. 57) as belonging to the New Zealand, Indo-Pacific, and Australian region.

The first work in which Acmæa was treated monographically was Haller's *Studien über docoglosse and rhipidoglosse Prosobranchier,* which appeared in 1894. This deals with one species of Scurria and three of Acmæa and as it treats all the important organs of the body except the shell, it would at first sight seem to render superfluous further work upon the small family of Acmæidæ. Various statements made by Haller have, however, been the object of vigorous criticism and in other particulars which

have not yet come under public discussion I have found myself unable to adopt his views or to confirm his observations. It is unfortunate that of Haller's four species three are incorrectly named (*cf.* Willcox, :00). One, *Scutellina galathea,* is in all probability an Acmæa but its specific name can only be surmised; for his two other Acmæas he employs the name Lottia, a synonym which was not only discarded by its author some sixty years ago but which has been since 1865 in use for another genus or subgenus, so that the Lottia of Haller is an entirely different animal from the Lottia of Carpenter and modern authors in general.

In 1898, appeared a brief monographic account by myself of *A. fragilis.* This paper dealing as it did entirely with preserved material which was studied almost exclusively by means of sections, left room for such completion and enlargement as is presented in the present work. In 1904, appeared an excellent paper on the anatomy of *Lottia gigantea* by W. R. Fisher to which I shall frequently have occasion to refer. The latest contribution is an article by Spillman in which (:05, pp. 553–564, 568–572) the heart and vessels of Acmæa are described.

Other papers which in the last decade have discussed the Acmæidæ have been occupied mainly with criticism of some of Haller's statements and with the presentation of counter observations. The chief matters in dispute have been the existence of a cœlom as distinct from the pericardial, nephridial, and gonadial cavities, the extent of the nephridium, the presence of a subradular organ. The chief disputants have been Haller, Pelseneer, Thiele, Willcox.

Methods

The first problem which faces any student of the Mollusca relates to narcotization. This is a much less important question among the limpets than in most other groups since the form of the body is such that no great amount of distortion can be effected even by the most powerful contraction. Proper extension of mantle and tentacles are the main results to be attained. For these purposes I have employed various methods — Epsom salts, cocaine, chloretone, stale sea water, fresh water. No one of these

methods was altogether successful. The cocaine — a 2% solution in 50% alcohol added drop by drop —produced extension of gill and cephalic tentacles. In specimens killed after this treatment, the subradular organ was likely to be extruded. Chloretone — crystals gradually added to sea water — produced at first a general extension but a larger dose brought about contraction. This agent is especially useful for narcotizing parts — as gills or tentacles — which it is desired to study while still alive. Extension of mantle tentacles is best obtained by killing in Gilson's fluid, extension of the mantle in general by this method or by allowing the animal to die in stale sea water, or, as recommended by Fisher, in fresh water.

The most satisfactory killing agents I have found to be picro-sulphuric acid, chrom-alcohol (equal parts of 70% alcohol and $\frac{1}{10}$% chromic acid), and corrosive sublimate with 5 to 20% of acetic acid. A weak — 5% — aqueous solution of sublimate preserves the external cilia better than a stronger one; this solution also I have employed with success for material in which it was desired to demonstrate mucus. The various osmic acid solutions — vom Rath's, Hermann's, Flemming's — have no marked superiority except for demonstrating certain glands as noted in the section on the integument. Picro-sulphuric acid has the advantage when used for very small specimens, of decalcifying the shell while leaving it *in situ*; in specimens killed in corrosive acetic the shell parts from the animal, in consequence I suppose of the pressure due to the more rapid evolution of gas brought about by the larger proportional amount of acid. An acid killing agent, as Bernard has pointed out, is desirable because it at once coagulates the mucus and thus renders the goblet cells more conspicuous.

For purposes of dissection it is desirable to have some specimens killed in formalin. The comparative transparency produced by this agent as well as its slight swelling action are often of advantage; it has the further good quality that it preserves at least for some time the color of the nephridial epithelium. A 2% solution is most satisfactory and it is of course desirable that the solution if acid should be neutralized. Opaque specimens for dissection are best killed in Gilson's fluid. It is perhaps unnecessary to add that details can often be made out better in specimens in which

the pressure on the viscera entailed by the contraction of the foot has been done away with either by removal of this organ or by slitting it lengthwise and thus opening the visceral cavity.

Sections were prepared by imbedding in paraffin, were stained usually with hæmalum and eosin or with Ranvier's picrocarmine and methylen blue, and were mounted in xylol balsam. For demonstration of mucus Mayer's mucicarmine was employed on sections of material killed in 5% sublimate solution. Endothelium was demonstrated by bathing the fresh membrane for half an hour in a mixture composed of four parts saturated aqueous solution of methylen blue and 96 parts $\frac{6}{10}$% salt solution, then leaving it for some hours in a saturated solution of ammonium picrate. Specimens thus prepared were mounted in glycerine saturated with ammonium picrate and have kept well for some years.

For macerations, good results have been obtained with Haller's fluid (*cf.* Lee's *Vademecum,* 4th ed., p. 318) and Bernard's fluid (Bernard, '90, p. 101).

Total preparations showing the innervation of thin structures like the mantle or the gill were most successful when stained with methylen blue and mounted in glycerine surcharged with ammonium picrate. Such preparations are fairly permanent.

Habits

Here should be intercalated the article on the biology of Acmæa already mentioned. To the facts there stated I have only to add that I have occasionally found in the nuchal cavities of specimens collected at Eastport tiny shells, measuring about one mm. in diameter which have been identified for me by Mr. Charles W. Johnson of Boston as in all probability the young of *Lacuna neritoidea* Gould. Whether these are commensals or merely accidental visitants I am not prepared to say.

The literature dealing with this section is incorporated in the list at the close of the present article. The statement by Dall that fertilization is internal was published not in 1879 but in 1882.

GENERAL DESCRIPTION

Acmæa testudinalis, like the limpets in general, has a somewhat dish-shaped shell, (Figs. 1 and 2), roughly conical in section and with a mouth (corresponding to the base of the cone) which is broadly oval though with the anterior part a trifle narrower than the posterior. The apex of the shell lies not over its center but about one third of the distance from the anterior end. It may be

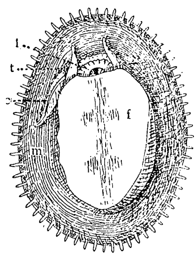

FIG. 1.

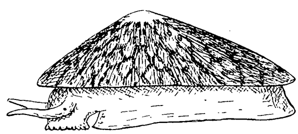

FIG. 2.

FIG. 1.—*Acmæa testudinalis.* Ventral view. × 1½. Whole animal with the exception of the mantle, strongly contracted. *c.*, ctenidium; *f.*, foot; *l.*, lip surrounding the circular mouth which is dilated to show the inner lips between which appears the dark radula; *m.*, mantle; *t.*, tentacle. Camera.
FIG. 2.—*Acmæa testudinalis.* Side view. × 1½. Camera.

worthy of mention that the true, or docoglossate limpets and the keyhole limpets (Fissurellidæ) differ in this respect from all the other widely dissimilar genera to which this form of shell is common and in which the apex, though varying in position in different forms, is never anterior. The condition in Acmæa is a secondary one for Boutan ('98, p. 1869) finds that in *A. virginea* the apex is at first posterior and only in course of development assumes the adult position.

In color the shell is usually yellowish gray marked with radiating stripes or tesselations of dark brown. The extent and the tint of the markings vary greatly and they are sometimes almost or quite absent. The hypostracum, or inner layer of the shell, stops a little short of its edge so that on the internal aspect the markings appear as a narrow border. This I understand to be the "more or less distinct internal border of the aperture," mentioned by Tryon and Pilsbry ('91, p. 5) as a character by which the Acmæidæ are

usually distinguished from the Patellidæ. While the family to which a limpet belongs may often be thus recognized, the genera at least of the Acmæidæ, cannot according to Pilsbry, be determined by a study of the shells alone.

In the living animal the mouth of the shell is almost entirely filled up by the foot, a broad fleshy expansion of the ventral body surface which apparently serves as a sucking disc[1] to hold the animal to the rocks on which it lives. The organ is composed chiefly of muscle fibers most of which run from the shell ventralward, spreading both laterally and toward the median line. A few fibers, however, are parallel with the sole and run either lengthwise or transversely. The fibers are imbedded in connective tissue and are entirely wanting near the margin of the foot, which is composed mainly of connective tissue excavated by large blood sinuses and is therefore extremely flexible. Certain marginal unicellular glands, whose secretion may aid the foot in clinging, are described, together with the epithelium in general, under the topic *Integument.* Just in front of the foot appears a ventral prolongation of the head, the muzzle; it bears on its tip the small circular mouth surrounded by the simple frill-like lip, which is characteristic of the subgenus Collisella. In a specimen which has been narcotized with chloretone the mouth is usually dilated enough to show the yellowish brown inner lips (Fig. 1) and in a fresh one its continual opening and closing permits a good view of the radula, which has a constant licking motion. It has been suggested by Davis and Fleure (:03, p. 49) that this movement serves to keep in motion the blood in the circumodontophoral sinus and thus reinforces the feeble ventricular muscles.

At the sides of the muzzle appear a pair of long and very contractile tentacles; they are borne on the posterior part of the head and each carries on the outer side of its base a simple optic pit which in the living animal or in a formalin specimen appears as a spot of black pigment.

In front of the head or at the right of the foot the ctenidium, or gill may usually be seen. When fully extended this organ is nearly

[1] This almost universally accepted view has been controverted by Davis ('95 ; Davis and Fleure, :03, pp. 4, 15) but the arguments do not seem to me conclusive.

one half as long as the entire animal; it is attached to the posterior wall of the nuchal cavity so that its distal end alone is visible (Fig. 3). It is a somewhat plume-like organ; the shaft of the feather is represented by a flattened triangular lamina, very long and very narrow, which bears on its flattened dorsal and ventral faces the structures corresponding to the barbs. These are two series of flattened more or less semicircular sacs each of which runs transversely across the shaft so that its cavity communicates with each of the two lateral vessels described below.

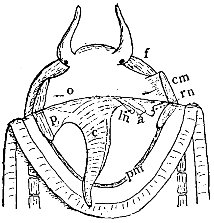

FIG. 3.— *Acmæa testudinalis.* Nuchal cavity. × 2. Columellar muscle cut and roof of chamber turned back. *a.*, anal papilla; *c.*, ctenidium; *cm.*, columellar muscle; *f.*, foot; *ln.*, *rn.*, left and right nephridial papillæ; *o.*, osphradium; *p.*, pericardium; *pm.* pallial muscle

Blood is conveyed through the gill by means of two vessels each of which occupies one margin of the shaft. That on the right edge conveys blood from the suprarenal plexus (*cf.* p. 184) to the gill, that on the left carries blood from the gill to the auricle. In the living animal the gill is usually so rotated that the efferent vessel alone is visible.

Attachment of the shell is effected by a band composed of the pallial and the columellar muscles (Fig. 4). The pallial muscle is ring-like and its fibers extend from the shell into the mantle. The columellar muscle is horseshoe-shaped and lies just internal to the pallial muscle from which it is separated by no sharp boundary; its fibers run from the shell into the foot and it is of course interrupted anteriorly where the head is interposed between these two structures.

From this muscle band depends the mantle, a thin, tentacle-fringed, membranous fold which lines the marginal part of the shell and in front of the columellar muscle runs up to the apex. In this region it forms the roof of a deep cavity, the nuchal cavity, which lies above the head and neck and is bounded at the sides and behind by the columellar muscle and the front part of the visceral mass. Elsewhere the mantle forms the outer wall of a groove-like space, the mantle groove, enclosed between it and the foot. Mantle groove and nuchal cavity are of course continuous; both together constitute the mantle cavity.

The dorsal part of the body is in the main developed into the convex visceral mass, but just above the anterior part of the foot it suddenly contracts into the neck (Fig. 2) and this, passing forward and slightly enlarging, gives rise to the head which curves ventralward and ends in the so called muzzle, thus bringing the mouth to lie flush with the foot. The head consists of a thin, muscular wall which in the region of the muzzle is fused with the pharyngeal walls but farther back is separated from them by a large blood sinus.

The visceral mass contains the digestive tract, blood vascular system, reproductive glands, and nephridia. It is covered by a green epithelium which immediately underlies the shell and may readily be brushed away. This being done, parts of all the above-mentioned organs may be made out through the thin body wall though they can be seen somewhat more readily in a specimen preserved in Gilson's fluid or formalin.

In such a preparation (Fig. 4) one notices first the band composed of pallial and columellar muscles; it is divided into a series of fascicles by blood vessels which cross it. External to the muscle ring is the mantle, fringed with its tiny tentacles and marked on the edge with a band of pigment whose alternations of light and dark tint have a general correspondence with the light and dark radial markings of the shell. In this region the mantle is thickened by the presence of a mass of unicellular glands of uncertain function. Just internal to the pigment band is a zone, often contracted to extreme narrowness, which represents the thin, non-glandular part of the mantle. Internal to the anterior curve of the pallial muscle and between the ends of the columellar muscle is a pellucid space, the roof of the nuchal cavity, in which may be noted traces of a blood plexus and through which the outlines of the ctenidium and the head may be more or less clearly seen.

Turning now to the visceral mass we note just internal to the columellar muscle and pericardium (see below) the edges of the generative gland; the bulk of the organ lies in the ventral part of the body directly above the foot, but its margins, especially the left one, curve dorsalward until they immediately underlie the nephridium through whose thin walls they are more or less clearly to be seen. Internal to the pericardium a small portion of the gland is

always distinctly visible. In the apical part of the visceral mass is the digestive gland; partly imbedded in it and partly lying between

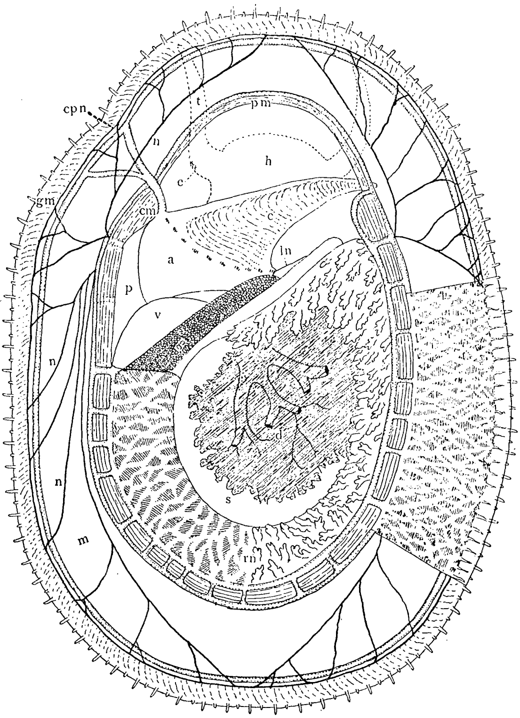

FIG. 4.— *Acmæa testudinalis.* Dorsal view with shell and superficial epithelium removed. × 4. *a.*, auricle; *c.*, ctenidium; *cm.*, columellar muscle enclosing the nuchal cavity and visceral mass; *cpn.*, circumpallial nerve ring; *d.*, digestive gland; *e.*, eye; *g.*, generative gland; *gm.*, glandular zone of mantle; *h.*, head; *ln.*, left nephridium; *n.*, mantle nerve; *p.*, pericardium; *rn.*, right nephridium, its cœca on the right half of the figure represented in profile, on the left half represented *en face* thus giving the effect of a vascular plexus; *s.*, stomach; *t.*, cephalic tentacle; *v.*, ventricle; the inner non-glandular portion of mantle is mostly represented as transparent but in a small section shows the vascular plexuses of which the ventral one underlies and obscures the external pallial vessel. The rectum, unmarked, lies between the generative gland and the right nephridium. For names of blood vessels see text. Two of the vertical interfascicular vessels are shown in dotted lines at the left; elsewhere they underlie and are obscured by the horizontal interfascicular vessels. Outlines drawn with camera, details combined from several specimens.

it and the generative gland are portions of the coiled alimentary tract especially the obliquely-running posterior end; sometimes a bit of the radula appears near the middle of the gland. On the left

side, abutting against the anterior portion of the columellar muscle is a pellucid triangular space, the pericardium. This space lies for the most part in the anterior, nearly vertical wall of the visceral sac and may in a preserved specimen of a ripe Acmæa be almost or quite hidden by the generative organ, which seems to overlie it. Such an appearance is, however, an artefact, being due to a folding of the anterior wall brought about by strong contraction. Behind the pericardium and abutting against the whole remaining extent of the columellar muscle lies the dorsal portion of the right nephridium; the ventral part of the organ occupies the right half of the ventral face of the visceral mass directly underlying the generative gland and is, of course, invisible from above. The marginal part of the dorsal nephridial wall is especially conspicuous for this is produced dorsally into numerous branched cœca that immediately underlie and are grown to the dorsal integument. Anteriorly the nephridium not only occupies the margin of the visceral sac but sends from its right limb toward the median line a large branched lobe which reaches and in part overlies the end of the intestine. On the left of the rectum between it and the pericardium, may be distinctly seen the small left nephridium, partly overlying the rectum.

The structures thus far described may, as has been stated, be made out more satisfactorily in a preserved specimen; the blood vessels now to be enumerated can be studied to much better advantage in a living animal though some of them are distinguishable in a preserved one. An Acmæa which has been kept in water of 15° to 25° C. until dead or dying is well relaxed. In such a specimen some at least of the mantle nerves may often be seen and it usually shows clearly the following vessels:—

1. Internal pallial vessel (*Mantelrandvene* or *Mantelrandarterie* of Haller), which lies just outside and beneath the pallial muscle and, like it, forms a complete ring.

2. Perivisceral vessel, a U-shaped vessel lying just inside the columellar muscle. On the right it is continued around the end of this muscle and across the pallial muscle to the internal pallial vessel; on the left it ends just behind the pericardium, where it falls into one of the horizontal interfascicular vessels.

3. External pallial vessel (pallial vein of authors), which forms

a second ring around the margin of the mantle at the base of the glandular zone.

4. The horizontal interfascicular vessels (*Quervenen* of Haller), a series of vessels which cross the columellar and pallial muscles connecting the perivisceral and the internal pallial trunks.

5. The vertical interfascicular vessels, a series of vessels which run up from the foot in the columellar muscle, join each with a horizontal interfascicular vessel and so connect with the internal pallial.

6. The mantle plexus. This consists of a dorsal and a ventral network. The vessels of the ventral network arise from the internal pallial trunk and the ultimate branches end blindly in the glandular zone. The vessels of the dorsal network arise from the external pallial trunk and end blindly in the non-glandular zone of the mantle. In a view such as we are describing the two networks are indistinguishable.

7. The transverse pallial vessels. One or two vessels, which arise from the external pallial trunk opposite the left end of the columellar muscle, unite (if two are present) and curve around the muscle to the auricle. In a relaxed specimen such as we are describing they cannot be traced to the auricle but in a perfectly fresh animal their pulsation is readily seen.

8. Indications of a suprarenal plexus (*periintestinales Venennetz* of Haller). The distal ends of the nephridial cœca are grown to the dorsal body wall and the blood sinus in which they lie is thus broken up into a series of connecting spaces.

9. Supravisceral vessels, which ramify over the dorsal surface of the digestive gland and open eventually into the suprarenal plexus. I have been most fortunate in finding these dorsal vessels showing clearly in specimens preserved in Gilson's fluid in which the contraction had been reduced to a minimum either by narcotizing with chloretone or by slitting the muscles of the foot.

10. Ctenidial vessels. In a preserved specimen one may see through the wall of the nuchal cavity the ctenidium with its dorsal series of lamellæ and the afferent and efferent vessels running respectively along its right (posterior) and left (anterior) edges. The afferent vessel brings blood from the suprarenal plexus, the efferent one carries it to the auricle. At the base of the gill may

be seen small opaque patches, the expression of interspaces between vessels that open directly into the auricle or the gill vessels. Those which open into the afferent vessel come from the anterior part of the suprarenal plexus; those which open into the auricle and the efferent vessel come from the nuchal plexus.

The nuchal cavity (Fig. 3), as has been said, lies in front of the visceral sac and above the head and neck; it is somewhat triangular in longisection and its posterior wall curves from side to side so that the cavity is much deeper from front to back in the median line than laterally. It contains the following structures, which with the exception of gill and pericardium are borne entirely on the posterior wall: pericardium with the enclosed heart, ctenidium, papillæ of small left and of large right nephridia, anal papilla. Separate generative openings are absent, as is also a hypobranchial gland.

On looking into the cavity from the front, one notices first the large ctenidium whose line of attachment runs along the mantle from the left tip of the columellar muscle obliquely back to the hinder wall of the cavity, where it ends a little on the right of the median plane. Through the thin posterior wall of the chamber can be seen the rectum lying near its dorsal edge and extending from the ctenidium almost to the right tip of the columellar muscle, where it ends upon a prominent anal papilla. Below the rectum appears a portion of the large right nephridium. It opens by a sizable papilla (infra-anal papilla of authors) located at the right of the anus. Above the rectum, in the triangle included between it, the gill, and the dorsal edge of the mantle cavity, lies the small left nephridium; it opens by an inconspicuous papilla (supra-anal papilla of authors) above and to the left of the anus. Behind and on the left of the ctenidium is a large triangular space enclosed between it and the columellar muscle and lying partly in the posterior and partly in the dorsal wall; this is the pericardium. The osphradia are so inconspicuous as to be readily overlooked; they are a pair of narrow transverse epithelial ridges which lie on the neck a little behind the anterior end of the columellar muscle. In a specimen whose shell was 35 mm. in length the left osphradium was 2 mm. long and the right 1.5 mm. According to Dall these structures are sometimes rendered conspicuous by an orange pigment; I have never seen such specimens.

Previous Investigations.— No extended account of the external anatomy of Acmæa has hitherto been published; the fullest description is embodied in a single paragraph by Forbes and Hanley ('53, p. 436). Haller's description of the mantle and gill will be discussed in subsequent sections.

LITERATURE

BERNARD, F.

'90. Recherches sur les organes palliaux des gastéropodes prosobranches. *Ann. Sci. Nat.*, zoöl., ser. 7, vol. 9, pp. 89–404, 10 pls.

BOUTAN, L.

'98. Sur le développement de *l'Acmæa virginea*. *Compt. Rend. Acad. Sci. Paris*, vol. 126, pp. 1887–1889.

BOUVIER, E. L.

'87. Système nerveux, morphologie générale et classification des gastéropodes prosobranches. *Ann. Sci. Nat.*, zoöl., ser. 7, vol. 3, pp. 1–510, 19 pls.

DALL, W. H.

'82. On certain Limpets and Chitons from the Deep Waters off the Eastern Coast of the United States. *Proc. U. S. Nat. Mus.*, vol. 4, pp. 400–414. (Date of volume 1881; date of paper, January, 1882.)

DAVIS, J. R. A.

'95. The Habits of Limpets. *Nature*, vol. 51, pp. 511–512.

DAVIS, J. R. A., AND FLEURE, H. J.

:03. L. M. B. C. Memoirs. X. Patella. London, 76 pp., 4 pls.

ESCHSCHOLTZ, F.

'33. Zoologischer Atlas. Fünftes Heft, herausgegeben von D. Martin Heinrich Rathke. Berlin.

FISHER, W. R.

:04. The Anatomy of *Lottia gigantea*. *Zoöl. Jahrb., Abth. f. Anat.*, vol. 20, pp. 1–66, 4 pls.

FORBES, E.

'39. On a Shell Bank in the Irish Sea considered Zoologically and Geologically. *Ann. Nat. Hist.*, vol. 4, pp. 217–223.

FORBES, E., AND HANLEY, S.
'53. A History of British Mollusca and their Shells. Vol. 2.

GEDDES, P.
'79. On the Mechanism of the Odontophore in Certain Molluscs. *Trans. Zool. Soc. London*, vol. 10, pp. 485–491.

HALLER, B.
'94. Studien über docoglosse und rhipidoglosse Prosobranchier. Leipzig, 166 pp., 12 pls.

PILSBRY, H. A.
'98. The Function of the Radula. *Proc. Acad. Nat. Sci. Phila. 1898*, p. 202.

SMITH, E. A.
:03. A List of Species of Mollusca from South Africa. *Proc. Malacol. Soc. London*, vol. 5, pp. 348–402.

SPILLMANN, J.
:05. Zur Anatomie und Histologie des Herzens und der Hauptarterien der Diotocardier. *Jen. Zeitschr. f. Naturw.*, vol. 33, pp. 537–588.

TRYON, G. W.
'82–'84. Structural and Systematic Conchology. Philadelphia.

TRYON, G. W., AND PILSBRY, H. A.
'91. Manual of Conchology. Vol. 13. Philadelphia.

WILLCOX, M. A.
'98. Zur Anatomie von *Acmæa fragilis* Chemnitz. *Jen. Zeitschr. f. Naturw.*, vol. 32, pp. 411–456, 3 pls.

WILLCOX, M. A.
:00. A Revision of the Systematic Names employed by Writers on the Morphology of the Acmæidæ. *Proc. Boston Soc. Nat. Hist.*, vol. 29, pp. 217–222.

WILLCOX, M. A.
:05. Biology of *Acmæa testudinalis* Müller. *Amer. Nat.*, vol. 39, pp. 325–333.